Life History of Austrosuccinea archeyi, an Annual Snail, and its Value as a Post-Glacial Climatic Indicator.

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Abstract.

A native snail, Austrosuccinea archeyi, first discovered in consolidated sand of post-Pleistocene age at Doubtless Bay, Northland, is now shown to be a still living species on coastal dunes, with a range from Spirits Bay to Mount Maunganui and as a fossil to as far south as Cape Kidnappers. This snail is found to have an annual cycle which correlates with rainfall. The extremely specialised habitat and narrow tolerance of these snails makes the fossil occurrences useful indicators of past xerophytic phases in respect to post-Pleistocene climate.

In 1933 I described a new species of land snail (Succinea archeyi) obtained from post-Pleistocene consolidated sands associated with "moa" remains (Euryapteryx geranoides and curtus) at Tokerau Beach, Doubtless Bay. The New Zealand snail is closely allied to the Recent South Australian Succinea australis Ferussac, 1821, which species Iredale (1937, p. 307) made the type of his genus Austrosuccinea.

In June, 1947, Mr. C. W. Devonshire, then of Lake Ohia Native School, reported that living *Austrosuccinea* were abundant during winter and spring just behind the fore-dune at the "planks," road access to Tokerau Beach, but that living examples entirely disappeared during the summer months. A personal visit to the locality in June, 1947 confirmed the presence of living *Austrosuccinea*.

ACKNOWLEDGMENTS.

I am greatly indebted to Mr. C. W. Devonshire for his original report and subsequent observations, to Mr. A. Hancox for monthly records and growth series taken over a period of from two to three years, and to Mr. D. G. Forsyth for similar observations whilst he was stationed near the locality. For useful data relating to other occurrences I am indebted to Messrs. J. D. H. Buchanan, of Havelock North, R. K. Dell, Dominion Museum, Wellington, and G. Williams, Mt. Maunganui.

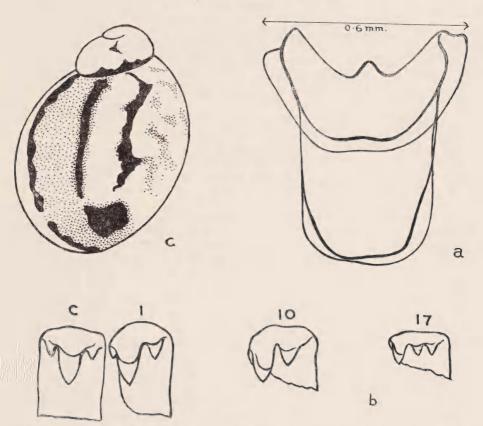
The rainfall records were generously made available by Dr. M. A. F. Barnett, director of Meteorological Services, Air Department, Wellington, and the botanical determinations by Mrs. Allen (nee Miss B. E. G. Molesworth), Miss U. V. Dellow and Mr. Robert C. Cooper.

The Generic Position of archeyi

Iredale's proposition of Austrosuccinea (1937, p. 307) is based primarily upon Quick's (1933, p. 312) statement that Victorian specimens (australis) resemble arenaria in jaw, radula and genitalia. Since then Boettger, 1939, proposed Quickella for the English-European arenaria, and Quick (1936, p. 42) has claimed considerable resemblance

between the South African striata and australis, special reference being made to the characters in common of less than twice as many marginal as lateral teeth and the large median projection on the jaw. In this later paper Quick disassociated australis and arenaria on the grounds that a penis sheath is present in the former but absent in the latter.

Pilsbry (1948, pp. 771-847) recognised the genera Oxyloma. Succinea and Quickella, but reduced Austrosuccinea to a synonym of Succinea on the grounds that the few diagnostic remarks made by Iredale were misleading. Nevertheless, there seems to be a good case for the recognition of Austrosuccinea in the light of Quick's (1936) remarks.



Text figure A. Austrosuccinea archeyi. a., Jaw; b., radula, showing central tooth, first and tenth laterals and number 17, a marginal. c. shows the mantle markings of an animal removed from its shell.

Summarised, the differentiating criteria for the several Succinid genera would appear to be as follows:

Penis provided with a sheath

Penis with a narrow appendix

Jaw with weak median projection only

Marginal teeth with long tapered bases

Four to five times as many marginals as laterals . . Oxyloma.

Penis without an appendix

Jaw with strong median projection and (usually)

lateral folds

Marginal teeth with long bases

Twice as many marginals as laterals Succinea

Jaw with strong median projection only Marginal teeth with broad shallow bases

One and a half as many marginals as laterals Austrosuccinea

Penis without a sheath

Jaw with strong median projection only Marginal teeth with broad shallow bases

Marginals and laterals few and of equal number . . Quickella

I have no preserved material of *australis*, but from Quick's excellent account of that species (1936, pp. 36-39) the New Zealand *archeyi* appears to be very similar.

The radula of *archeyi* shows a slight difference from that of *australis* in that the cones are shorter. The radula formula $15+10+1+10+15\times 90$ is almost identical with that of *australis*, which according to Quick is $16+10+1+10+16\times 90$. It appears also that *australis* is not restricted to a sand-dune habitat, but occurs inland also.

Quick (1936, p. 37) described very different mantle markings for australis from those found in archeyi. He described the mantle in australis as dark and opaque with a faint indication of mottling at the periphery and with a few yellowish-white chalky spots. In archeyi there is a sparse pattern of several dark intermittent narrow axial streaks with a large dark rectangular patch near the lower front margin of the mantle (Text fig. Ac.).

It is of interest also that Quick (1933, p. 310) records the English arenaria as living on damp circular depressions in sand dunes and that Pilsbry (1948, p. 843) describes the habitat for the eastern North American members of this genus (Quickella) as living in small thickets in the sandy shore zone.

That an annual cycle is not peculiar to the New Zealand species is shown by a note under Oxyloma decampi gouldi Pilsbry (1948, p. 782), a New England Succinea that frequents the aquatic vegetation of muddy ponds, river margins and ditches. "Probably most of the large individuals die by the end of summer, as I have often found only half-grown shells in autumn where large ones were found earlier in the season."

Habitat

The habitat of Austrosuccinea archeyi is extremely specialised, for the species occurs on a substratum of fine textured loose sand (fine quartz-sand at most places) only on or in the vicinity of the first and second dunes, parallel to the beach, usually in a narrow belt not more than 100-200 yards wide, and only where the original rather sparse native plant cover remains intact. That is the "Sand-grass Dune Community" to the "Scrub Dune Community" of Cockayne (1928, pp. 92-93).

The natural shade or shelter plants of the Austrosuccinea habitat are Cassinia retorta A. Cunn., Spinifex hirsutus Labill, and more uncommonly Coprosma acerosa A. Cunn. and Muchlenbeckia complexa Meissn. Two introduced plants add to the cover in certain areas (Taipa Beach): lupin, Lupinus arboreus Linn. and a Mediterranean grass, hare's tail, Lagurus ovatus Linn.

The food plants essential to the snails are a blue-green alga Anabaena variabilis Kutz (Cyanophyceae), which is available only during the wet months, and the outer tissue and finer roots of the Spinifex during the dry months, when the Anabaena dries and disappears.

Observations by Mr. Hancox show that *Anabacna* is in a lush state from May to August, is more or less dessicated during September to early October, dries up and is dispersed by winds from October to March and new growth appears again with the rains during March or April.

LIFE HISTORY

Food, or its availability, which is governed by moisture, controls the growth and life span of *Austrosuccinea archeyi*. These snails hatch from between June and August and reach maturity, just under 13 mm. in height, within twelve months, all adults dying between August and October of the year following their birth.

Young snails tide over the dry months of late spring and summer by partial aestivation, during which they keep alive with difficulty—but add little to their growth. They lie dormant in the sand around the roots of *Spinifex* and sealed by an epiphragm during dry periods, but will emerge and feed during rains. The alga has by this time disappeared, and until the new growth appears in March or April the young snails have only the food afforded by the *Spinifex*. Since hatchings occur over a period of two months in the spring and heavy mortality results from abnormal dry periods the size ranges vary from year to year for this reason. Fully grown living adults, however, can only be obtained from July to the end of September.

A prolonged dry summer results in a very late commencement of adult growth, but under such conditions growth seems to be accelerated when the rains commence and full adult size obtains before the end of August, the regular time for the dying off of the adult population. It was noticed that even during an abnormally wet spring the adult mortality took place in spite of the fact that the algal food was still in good supply. The life cycle of the snail is thus shown to be geared to the average conditions.

I have not yet managed to visit any of the colonies of the snails during the breeding months, but Mr. A. Hancox noted copulation and eggs on 28th April, 1949, and Mr. C. W. Devonshire recorded the deposition of eggs in clusters of up to fifteen on 16th July, 1947. He described the individual eggs as spherical and approximately 1 mm. in diameter and that they were attached to the thallus of the alga.

An egg associated with snails preserved in alcohol and collected by Mr. Hancox on 28th April, 1949, had a diameter of 1.75 mm. It was spherical with a large yolk which was slightly yellowish with a fine irregular network of faint lines, not reticulated. The yolk was surrounded evenly by a covering of clear jelly.

Monthly size log for Austrosuccinea

	Smallest	Average	Largest	Locality	Remarks
Jan. 2, 1949	2.50	5.00	6.75	To.	
20, 1948	4.00.	6.00	8.50	To.	
Feb. 12, 1949	2.75	5.00	7.50	To.	
Mch. 21, 1949	6.50	7.25	8.30	S.	+
April 25, 1950	6.50	00.8	9.00	Ta.	
28, 1949	6.00	9.50	10.50	To.	
May 25, 1950	5.50	8.50	9.25	Та.	
27. 1949	7.00	10.50	11.75	Ta.	
27, 1949	7.25	9.00	10.75	To.	
June 6, 1948	7.50	10.00	11.50	To.	
10, 1949	7.75	9.50	10.30	To.	(40% dead)
19, 1947	7.50	9.00	10.50	To.	
25, 1950	7.20	8.75	9.00	To.	
July 14, 1949	7.10	8.50	11.75	To.	(80% dead)
Aug. 2, 1947	8.25	11.00	12.25	To.	(maximum)*
3, 1948	7.50	10.00	10.75	To.	
25, 1948	6.75	10.00	11.50	To.	
Sept. 19, 1948	8.50	9.00	10.50	То.	(mostly dead)
Oct					(all adults dead)
Nov. 3, 1948	2.00	5.50	7.75	To.	(new generation)
Dec. 9, 1949	2.50	4.50	7.60	Ta.	
12, 1948	3.50	5.50	7.00	To.	

(To. = Tokerau Beach, Ta. = Taipa Beach, S. = Spirits Bay, + = abnormally wet season.)

Maximum sized dead example 13.00 mm. (To. 3/8/1948).

*Maximum sized living example, 12.25 mm.

Although the above records are rather intermittent the rapid winter growth curve, which corresponds with the availability of *Anabaena*, the adult mortality period from August to the end of September and the appearance of the new generation in November, are all very clearly shown.

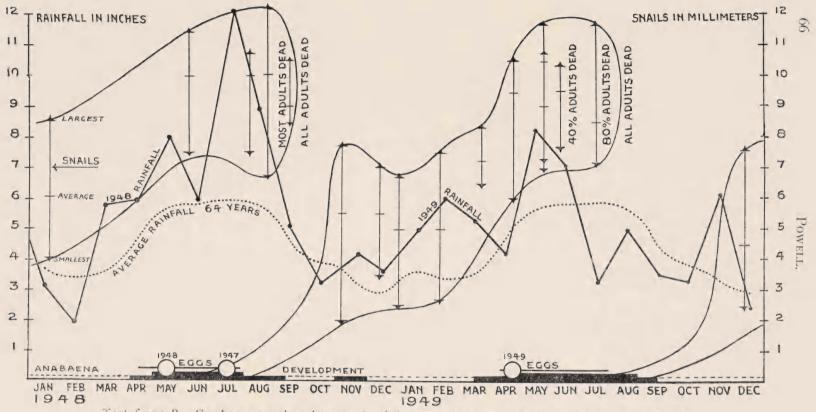
The monthly size ranges show variation from year to year, but this is resultant from a variable rainfall, year to year, as shown by the following table and in text figure B.

Rainfall in inches at Mangonui

1947 1948 1949	.94 3.10	.65 1.87	2.78 5.70	7.89 5.87	5.27 8.00	7.61 5 88	10.46 12.08	5.21 8.86	6.12 5.05	3.91 3.21	6.09 4.21	6.20 3.63	Annual 63.13 67.46 59.72
Average 64 years	3.72	3.39	3.57	4.64	5.66	5 79	5.92	5.76	4.57	3.96	3.28	2.98	53.24

These records were kindly supplied by Dr. M. A. F. Barnett, Director of Meteorological Services, Air Department, Meteorological Branch, Wellington.

It was remarked that over the period of 64 years at Mangonui, a rainfall of 12.08 inches (July, 1948) has only been exceeded once in July, and that was in July, 1946.



Text figure B. Graph representing the growth of Austrosuccinea generations over two years plotted against rainfall for the relevant years shown in relation to the average rainfall curve for 64 years. The period of egg laying is shown below and the relative abundance or absence of the alga Anabaena. The vertical lines with arrow points represent the minimum and maximum sizes respectively and the cross bar the average size for each dated sample examined.

Living Colonies of Austrosuccinea

- Spirits Bay, 1-3½ miles S.W. from Kapowairua, A. Hancox, R.A. and H. S. Prouse and A.W.B.P., 21/3/1949. The alga (Anabaena) was abundant and fully developed as in mid-winter, owing to an unusually wet summer season. The maximum size was 8.30 mm., which is large for this time of the year but resultant from a phenominally early growth of Anabaena. The colonies of snails, which were quite prolific, were under the shelter of Coprosma accrosa A. Cunn. and Muchlenbeckia complexa Meissn.
- Tokerau Beach, Doubtless Bay, C. W. Devonshire, D. G. Forsyth, A. Hancox, A. C. O'Connor and A.W.B.P., 1947-1950. Distributed intermittently between the first and second coastal dunes over the entire length of the beach. The most accessible colony is at the "planks" or road access to the beach. Very extensive fires during the summer of 1950 have taken heavy toll of the colonies. The shelter plants are Cassinia retorta A. Cunn., Spinifex hirsutus Labill, and more uncommonly Coprosma acerosa A. Cunn. and Muchlenbeckia complexa Meissn. This paper deals largely with the material collected and observations made at this locality over the period from June, 1947, to July, 1950.
- Taipa Beach, Doubtless Bay, A. Hancox and A.W.B.P., 1949-1950. A flourishing colony occupies the fore-dune over the western half of the beach. There is rather more shelter than in other more natural locations owing to the addition of two vigorous introductions, the hare's tail grass, *Lagurus ovatus* Linn, and the lupin, *Lupinus arborcus* Linn.
- One mile north of Tauranga Kawau Point, between Whananaki and Mimiwhangata, A.W.B.P., 27/10/1947. The remains of what had been a living colony of snails a few months earlier occupied only a few square yards of the foredune. The shelter plants were very sparse, only Cassinia retorta and Spinifex hirsutus, the latter being quite dead. The Anabaena was still moist and fleshy where it was under cover. Grazing sheep had so reduced the plant cover that it is doubtful if this colony still exists.
- Mount Maunganui, Bay of Plenty, in coastal dunes several miles east-ward along the beach. Living examples were taken by Mr. G. Williams in 1947, but a recent search (Aug., 1950) failed to locate the species either alive or dead.

Extinct or subfossil colonies of Austrosuccinea

1. On rounded, almost detached headland one mile south of Cape Maria van Diemen (mainland). R. Michie and A.W.B.P., 17/11/1948. This headland has a thick cover of 15 to 20 feet of consolidated wind-blown sand on a base of hard rock. At present most of the top of the headland is in rough grass fringed with flax (*Phormium*) and a stunted area of coastal scrub down the almost perpendicular seaward face. On the landward side there is only drifting sand and bare rock with no vestige of plant cover. Erosion of the consolidated sand in several places reveals fossil Austrosuccinea in a

band one to ten inches below the surface, and scattered for some feet deeper are fossils of *Rhytida duplicata* and a *Placostylus* ancestral to a living new subspecies which occupies the scrub area of the seaward cliff.

The sequence revealed by these occurrences suggests an early cover of coastal scrub with *Placostylus* and *Rhytida* followed by a dry period when the scrub disappeared from all but the seaward cliff, and the headland was overwhelmed by blown sand. Then the process of consolidation under more moist conditions, the development of the Sand-grass Community allowing advent of *Austrosuccinea* and now the development of the Shrub-dune Community modified by grazing stock. The now complete cover of the sand on the headland excludes *Austrosuccinea*, which apparently only exists under xerophytic conditions.

2. On a small island directly south of the most northern headland block at Cape Maria van Diemen mainland, A. Hancox and A.W.B.P., 18/11/1948. This island has been completely burned off and is now covered by a rank growth of "spiny clover."

Remains of Austrosuccinea and Placostylus ambagiosus worthyi Powell are abundant in the surface layer of ash and humus. The sequence here has been from coastal scrub to a Sand-grass dune Community, but the cover of blown sand is slight compared with the first locality. Succession from the xerophytic phase has been obscured by recent fires, but the charred remains of stunted Metrosideros and Coprosma indicate a normal development to the Sandscrub Community.

3. The "Placostylus ambagiosus priscus block" occupying the high dune and "bad-lands" area lying about 1 mile to the south of the N.W. Cape Maria van Diemen mainland headland and the Werahi Stream and including the high dune of Herangi, 700 feet. The south-west corner of this block is of consolidated light brownish sand and produces fossil remains of Paryphanta watti, Rhytida duplicata, Serpho kivi an arboreal snail, and Liarea n. sp. as well as vast numbers of Placostylus ambagiosus priscus. The presence of the former indicates a contemporary condition of dense coastal rain forest. The mode of occurrence of the snails at this locality (Bartrum & Turner, 1928, pl. 21, fig. 7) is exactly as those found living at Unuwhao, 700-900 feet, between Spirits Bay and Tom Bowling Bay. Meandering lines of Placostylus as they occurred nestled in along roots and under Astelia, Liarea in circular patches suggestive of their association with Carex clumps, and the sporadic occurrence of Paryphanta watti are all indicative of a natural forest community suddenly overwhelmed by advancing sand dunes. That the underlying consolidated sand was capable of supporting a coastal rain forest is thus indisputable, as also is the inference that the climate must have been much more moist than now. Now the vegetation in the block is restricted to a sparse covering of scrub with flax (Phormium) and toetoe (Arundo kakaho) only on the top of Herangi. Here again the deterioration to xerophytic conditions is

shown by marginal occurrences of fossil Austrosuccinea. Burning of the area by the former Maori occupants and subsequently by settlers has undoubtedly hastened the destruction of the vegetation and allowed mass movements of sand.

It is interesting to note that a map of the area prepared by T. K. Thompson in 1895 and now in the Lands and Survey Office, Auckland, shows a covering of "fern, manuka and scrub" between Herangi and the West Coast (i.e., No. 1 locality). This traverses the middle of the *priscus* colony where the heavy rain forest formerly stood. Further, a photograph taken by W. H. Winkelmann in 1902 from Cape Maria van Diemen Island shows the whole of this area to the upper slope of Herangi to be devoid of vegetation as it is today.

- 4 North-western end of Tokerau Beach, Doubtless Bay, G. Archey and A.W.B.P., February, 1932. Type locality for the species, which was found abundantly as a fossil with "moa" remains. Other fossil land snails in the consolidated dunes, notably *Rhytida dunniae* and *Phenacharopa novoscelandica*, indicate a former coastal forest cover. Living *Phenocharopa* elsewhere in the north is found only in the very damp innermost recesses of tall nikau (*Rhopalostylis*) stands.
- 5. Sand dunes 1½ miles south of Ngunguru, A.W.B.P., 1934. Bleached shells are encountered in loose sand drifts. A Shrub-dune area exists nearer to the Ngunguru river and the alga *Anabacna* is abundant, but no living *Austrosuccinea* were located.
- 6. Occan Beach, Whangarei Heads, R. K. Dell, Jan., 1938, bleached shells in coastal dunes.
- 7. In consolidated sand at the back of the dunes, Oneroa, Waiheke Island, Auckland. K. Hipkins, 1946. The outcrop has since been destroyed by building activities.
- 8. Ocean Beach, five to six miles south of Cape Kidnappers in fixed dunes, about 100 yards from the beach, together with fossil *Rhytida spelaca* Powell: J. D. H. Buchanan.

Age significance of the subfossil occurrences

It will be noted from the above list and chronological table (following) that the same climatic sequence is shown in each locality. That is, a former moist climate allowing of a coastal rain forest on beach flats, followed by a presumed dry period when the coastal forests died and allowed the formation of drifting dunes and the development of a Sandgrass Community with Austrosuccinea and ultimately the elimination of that species under natural conditions with the succession to the fully developed Shrub-dune Community. In most cases, however, the advent of grazing animals, fires and other human interference has intervened between the development of these two communities.

70 Powell.

The dating or correlation of the New Zealand periods of climatic change with those of the more fully known European sequence is conjectural.

Raeside (1948, pp. 153-171) dated the Canterbury warm forest period from between the seventh and the fourteenth centuries A.D. He also drew attention to the Report of the Committee on Glaciers for 1945 (Trans. Amer. Geophys. Union, 27, p. 219), in which it was postulated that the causative climatic variations affected both hemispheres simultaneously and not in alternation and therefore it is reasonable to suppose that the same pronounced Post-Pleistocene variations and the major Pleistocene variations were also synchronous in the two hemispheres.

One other line of evidence has a direct bearing upon the Northland climatic sequence, and that is the occurrence in raised beaches of the bivalve mollusc *Anadara trapesia*.

This is a gregarious species living partially buried on inter-tidal mudflats. It occurs living in the subtropical waters of Queensland, New South Wales and the Great Australian Bight, and as a fossil in South Australia, Victoria, Tasmania and Northern New Zealand. Its present restricted distribution is considered to have been due to refrigeration, the habit of living partially exposed to the atmosphere making it an easy victim to a sudden drop in temperature.

It is worthy of note that odd worn valves of this species occur in slightly raised beds of coarse shelly shingle underlying the foredunes both at Spirits Bay and at Tokerau Beach. These shingle beds must have been deposited during the first post-glacial period, when they received their covering of wind-blown sand that later consolidated during the warm, humid, second period, allowing of the growth of coastal rainforest. Crocker and Cotton (1946, pp. 64-82) discuss Australian Anadara occurrences at some length and conclude, quoting Professor David, that the last Australian cold phase was from three to ten thousand years past and that the period of maximum aridity in South Australia may have been as late as three thousand years ago.

I have just received a paper by W. F. Harris, "Climatic Relations of Fossil and Recent Floras" (1950), pp. 53-65), in which the following chronology is suggested:

Recent or Holocene

- Period 1. First post-glacial period to about 5000 B.C. (= Northern Boreal). Increasing warmth and comparative aridity.
- Period 2. Period of maximum warmth, 4500-500 B.C. Greater portion of this period humid (= Atlantic), latter part dry (= Sub-Boreal).
- Period 3. Cooler and moister climates lasting to the present day. Rainfall higher than now until a few centuries ago. (= Sub-Atlantic.)

Apparent sequence for four Northland Austrosuccinea sites

1	2	3	4	
Headland 1 m. S. of Cape M. v. Diemen		N.W. headland Cape M. v. D. (mainland)	Spirits Bay dunes 1-4½ m. S.W. from Kapowairua.	
Sh-dune with Pl. 1.	Drifting sand overwhelming Shdune at Herangi.	Shdune	Sgdune with A.	Present.
Sgdune with A. Shdune with Pl. 1.	Sgdune with A. Shdune with Pl. p.	Sgdune with A. Shdune with Pl. c.	Sgdune with A.	Period III: as now. A.D. to Present: more moist.
Coastal f. with Pl. 2.	Rain f. with Pl. p., Pa., R.S. & L.	Coastal f. with Pl. W.	Shdune - Sgdune with Pl. 3 (dwarf) coastal f. with Pl. S.	Period II: dry. 4500-500 B.C.: warm humid.
ROO	of older consolid CK FOUNDAT cleanic Whangal Trias Jura)	* * Anadara in raised shelly beach under- lying dunes.	Period I: comparative aridity5000 B.C.: increasing warmth.	
				Pleistocene.

(Abbreviations: Sg.-dune = Sand-Grass Dune Community; sh.-dune = Shrub-Dune Community; f. = forest; A = Austrosuccinea; L = Liarea n. sp.; Pl. 1 = a living new subspecies of Placostylus ambagiosus; Pl. 2 = a fossil ancestral form of Pl. 1; Pl. 3 = a new fossil subspecies or form of the ambagiosus spiritus group. It is dwarfed and obviously lived under xerophytic conditions; Pa. = Paryphanta watti; Pl. c. = Placostylus a. consobrinus; Pl. p. = a. priscus; Pl. s. = a. spiritus; Pl. w. = a. worthyi; R. = Rhytida duplicata and S. = Serpho kivi.)

Note.—The asterisks in the column for locality 4 denote the absence of consolidated sands at this site. It is presumed that the *spiritus* colonies were originally associated with consolidated sands, but these have since broken down and become loose and drifting with the fossil snails lying on or near the surface.

Study of the above table reveals an alternative possibility, and that is the assumption that the Northland formerly rain-forested coastal dunes were contemporary with the Canterbury warm forest period, referred by Raeside to Period III between the seventh and fourtheenth centuries A.D.

However, it is much more likely that these consolidated dunes had their origin in the comparatively arid Period I and received their rain forest cover during the succeeding warm humid period of 4500-1000 B.C., for the Northland sequence seems to indicate that the moist early centuries of Period III had a rainfall only sufficient to support a Shrub-dune Community.

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Composite photograph of Taipa Beach, looking north-west. Austrosuccinea lives under Spinifex (left foreground), Pimelia (right foreground) and Cassinia (middle right margin), but only on and in the vicinity of the foredune. The scattered dark patches on the sand are the dried-up remains of the alga Anabaena and the pale spots the flower heads of the introduced hare's tail grass, Lagurus ovatus. 20th January, 1950.